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EFFECTIVENESS OF SELECTION BY OWLS OF DEER-MICE (*PEROMYSCUS MANICULATUS*) WHICH CONTRAST IN COLOR WITH THEIR BACKGROUND

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INTRODUCTION

ALTHOUGH it is generally agreed by biologists that natural selection must play an important role in the evolution of protective coloration and of the other adaptations of animals, only a few measurements have been made of the actual effectiveness of selection under any particular set of conditions. Many students of evolution have in recent years come to assume a very low effectiveness for natural selection. Sewall Wright (1940 : 178), for example, doubts that the mutations which are important in evolution produce a sufficiently large selective difference to be demonstrable in the laboratory.

Should the selective advantage of adaptative characters, however, be in general very low, then the resulting rate of evolution must be very slow, too slow probably to account for the evolution of our existing plants and animals during the estimated period of geologic time. Moreover, unless selection is very effective, at least at some times and in some places, there is difficulty in explaining the demonstrated instances of the rapid origin of races and species in certain localities. The only alternative to effective selection seems to be the hypothesis of Goldschmidt (1940) of large and successful saltations, but this hypothesis has not generally been accepted by biologists.

In order to secure a measure of the possible rate of selection under controlled conditions I began a series of laboratory experiments in 1938, using various owls as predators and deer-mice (*Peromyscus*) of various colors as prey. Some preliminary experiments were conducted in outdoor runs. It was early discovered, however, that light intensity played an important role in the activities of the deer-mice. The experiments were then moved to a reaction room, specially constructed for the study, inside the Vertebrate Biology Building on the University of Michigan campus.

In the reaction room the owls proved to be able to capture living deer-mice in complete darkness, presumably by the sense of hearing. The lower limit of illumination under which the owls could find their prey by sight was, therefore, determined by the use of dead mice (Dice, 1945). Attempts were next made to set up an experimental situation reproducing so far as possible the conditions in nature under which the owls capture their living prey. After many discouraging failures a mouse "jungle" was designed which, it is believed, simulated fairly well, but in a simplified and standardized manner, the conditions in the natural habitats of the animals. By the use of this "jungle" a measure was obtained of the tendency of the owls to select those mice which are most conspicuous in color when viewed against the soil or other objects. These experiments were completed in August, 1945.

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SELECTION INDEX

As a measure of the effectiveness of selection in any given situation I propose the use of a "selection index." Where two types of individuals are equally abundant in an experimental population and are then exposed to predation or to some other form of mortality, both types should, if there is no differential selection, be taken in equal numbers. Should one type be taken in greater numbers than the other, this will indicate that selection is operating. If a and b, respectively, are the numbers taken of the two types A and B, then the relative selection in favor of or against type A will be measured by the difference between the observed value of a and its expected value $\frac{1}{2}(a+b)$, this difference being divided by $\frac{1}{2}(a+b)$:

$$\text{Selection index} = \frac{a - \frac{1}{2}(a+b)}{\frac{1}{2}(a+b)} = \frac{a-b}{a+b}.$$

The selection index evidently may vary between $+1.0$ and -1.0, being 0.0 when there is an absence of selective effect.

The significance of the deviation of the selection index from 0.0 may be tested by the usual chi-square formula for a 1 : 1 ratio:

$$\text{Chi-square of selection index} = \frac{(a-b)^2}{a+b}.$$

The formula given above for the calculation of the selection index applies, of course, only to a situation in which the numbers of the two types of prey are equal at the time when selection occurs. To measure the selection that occurs in situations where two or more types of prey are unequal in abundance, as will often occur in nature, more complex formulas would have to be developed.

In the experiments hereinafter described, the proportional numbers of the two types of prey exposed in any trial did in fact differ as soon as any individual had been captured by the predator. This difference in the available numbers of the two types of prey would decrease the selective pressure against the type taken most frequently and would depress the selection index toward zero in all those trials in which the predator took more than a single individual. In no case, therefore, will this source of error in the calculation of the selection index invalidate the conclusions reached. On the contrary, the true selection indexes would have been slightly higher than those calculated if the numbers of the two types of prey offered to the predator could have been kept precisely equal each time he made a selection.

The selection index obviously is a measure only of the selective advantage enjoyed by a particular phenotype under the conditions specified. The selection index is, therefore, a very different statistic than the selection coefficient (Haldane, 1932: 97; Wright, 1940: 165). The selection coefficient is calculated from the changes in the gene frequencies from generation to generation in the population under study. In the experiments here described the genotypes of the animals tested were unknown and the selection coefficients cannot be calculated.

EXPERIMENTAL METHODS

In my attempts to measure the effectiveness of selection under controlled laboratory conditions, I used several species of owls as the predators, and deer-mice (*Peromyscus maniculatus*) were used as the prey. The experiments were conducted in the same reaction room in which the minimum intensities of light under which owls are able to find dead prey were determined previously (Dice, 1945). This room is divided by a low partition two feet high into two compartments, each about nine by ten feet in size. Special lamps placed over the middle of each compartment make possible the control of the light intensities. The several types of soils used on the floors of the experimental compartments either matched closely or contrasted with the pelage colors of the mice being tested.

Each "trial" in one of these experiments consisted of exposing four live mice of one color and four of a contrasting color together in one compartment for a fifteen-minute period. In each experiment the colors of the mice and of the soils were arranged so that one kind of mouse matched the color of the soil in one compartment and the other kind of mouse matched the color of the soil in the other compartment. The mice were exposed alternately on the two colors of soils by using first one and next the other compartment. In every experiment, therefore, each kind of mouse was exposed an equal number of times on soil which it matched in color and on soil with which it contrasted in color. Furthermore, at the beginning of each trial the owl had the choice of the same number of mice of the two pelage colors, one kind matching the color of the soil and the other contrasting with it.

The mice were kept in the same room with the owl for a number of nights before being used in an experiment. It has been our experience that a mouse under these conditions quickly becomes frightened of the owl and will attempt to keep out of its reach if possible. In all the experiments in which the "jungle" was used the door of the nest box in which the mice were kept was opened at the beginning of the experiment and the animals were free to go out under the jungle or to remain in their nest box.

The trials were nearly all carried out in the morning, after the reaction room had been illuminated during the night by the fairly bright light of six 150-watt Mazda bulbs. Each trial period lasted for fifteen minutes, during which time the mice were exposed to the owl at the specified light intensity. Then the bright lights were turned on; the owl was driven back to his box, the door of which was then closed and the remaining mice were counted. If the owl had captured one or more mice, the carcasses usually were evident. If the owl had not captured a mouse, a second trial often followed immediately, usually at a different light intensity from that of the first trial. Rarely three, and still more rarely four, trials at different light intensities were given in a single morning. After the owl had captured a mouse in a given trial, the operations were discontinued for the day. Fairly dim lights then illuminated the room until noon, when all uneaten carcasses were removed. During the afternoon the room was kept in total darkness until 6 P.M., when the bright lights were automatically turned on again by a time clock.

By this artificial reversal of the usual cycle of day and night, the owl was always hungry in the morning and the mice began to move about and to expose themselves as soon as the bright lights were turned off in the reaction room at the beginning of each trial period.

Photometric Measurements

All the color measurements for this study, both of soil color and of pelage color, were made with a photovolt reflection meter, model 610. This instrument is manufactured by the Photovolt Corporation of New York City. The color reading is made by a movable search unit which is connected with the body of the instrument by a multiple electric cord. A concentrated beam of light from a small electric bulb in the search unit is reflected from the specimen at an angle of approximately forty-five degrees to a circular photoelectric cell which surrounds the light beam. The photosensitive cell when stimulated by this light produces sufficient electric current to be read on a sensitive galvanometer. A constant-voltage transformer forms part of an instrument to prevent fluctuations in line voltage from affecting the accuracy of the readings.

The area of specimen surface measured by the reflection meter, as adapted for this study, is a rectangle 9.3 by 7.5 millimeters. These are the dimensions of an opening in a blackened metal plate which is fastened over the face of the search unit. This plate was not supplied by the manufacturer, but was added by us. The opening in the metal plate is on the face of the search unit in such a position that it passes the brightest part of the light beam.

In order to locate precisely the area on the specimen to be read by the search unit, an additional finding device is necessary. This device also was constructed by us. A two- by two-inch square, lantern-slide cover-glass was mounted on the face of a small, square, wooden frame, whose outside dimensions were the same as the diameter of the search unit. Scratches were made on the glass plate to outline an area coinciding in dimensions and in position with the opening in the metal plate on the face of the search unit. A larger wooden holding frame was also constructed with inside dimensions that allowed it to fit loosely around the outside of the finding unit. Because the finding unit has the same outside dimensions as the search unit, the holding frame also fits loosely around the outside of the search unit. The search unit, however, is round, whereas the holding frame is square. A notch is therefore provided on one side of the holding frame to receive the projecting end of the glass filter inserted into the search unit, thereby keeping the search unit always oriented in the same direction in respect to the finding unit.

The specimen to be measured is placed flat on a table with the surface to be read facing upward. The finding unit is then placed on the specimen and moved about until the scratches on the glass plate of the unit enclose the exact area desired to be read. The holding frame is next placed outside and around the finding unit. Care is taken not to move the position of this frame when the finding unit is removed. The search unit is then placed in position, replacing the finding unit, and the reading is made.

Three color filters, red, green, and blue, furnished with the instrument, were used in making the photometric readings. The total light reflected from any one of these filters and reflected from a freshly scraped, white, magnesium carbonate block was taken as 100. The needle of the galvanometer was set at zero when the light from the search unit was projected into a hollow, black-lined cylinder of paper. Each reading of the galvanometer, therefore, is actually the percentage of light of the given color reflected from the specimen as compared to the amount reflected from the standard magnesium carbonate block.

Soils

Three types of soils were used in the various experiments to cover the floors of the compartments in which the mice were released. The "silica sand" employed is a commercial product that is nearly white. The "gully soil" has a dull, slightly yellowish gray color. It was taken from a small eroded gully near the Vertebrate Biology Building. The "Ann Arbor sand" is a building sand from one of the commercial sand pits in the vicinity of Ann Arbor. This sand is a mixture containing grains of several sizes and colors. Particles of gray are most numerous, but many other particles are black. This sand is in general appearance darker and less buffy in hue than the gully soil.

The reflection meter readings of the colors of these soils given in Table I are each the mean of fifteen or more readings of air-dry soil, each reading being taken on a different spot on the sample. The soils were very uniform in color and in shade and the reflection meter readings did not vary more than about one or at most two units on either side of the mean.

TABLE I

Colors of Soils Used in the Experiments with Owls and Deer-mice

Means of fifteen or more color readings.

Type of Soil	Mean Reflection Meter Readings		
	Red	Green	Blue
Silica sand	53	46	36
Gully soil	39	25	16
Ann Arbor sand	33	22	15

It will be noted (Table I) that the silica sand is much paler in color than either of the other two soils used in the experiments. This is shown by its higher readings for all color screens. The gully soil has higher readings for red and for green than has the Ann Arbor sand, but does not differ very much in the reading for blue. This indicates the more reddish buffy hue of the gully soil as contrasted with the Ann Arbor sand. In general shade the Ann Arbor sand is only slightly darker than the gully soil.

Predators

Two species of owls served as predators in these experiments: a male long-eared owl (*Asio wilsonianus*) from Pennsylvania and a male barn owl (*Tyto alba pratincola*) from southern Michigan. These were two of the birds that were used in my previous experiments on the light discrimination of owls (Dice, 1945). Both owls were fully adult.

About a fifteen-minute period seems usually to be required for an owl of either of these species to catch and completely to eat a mouse. However, an owl sometimes caught two or more rarely three mice in a fifteen-minute period, and one once took four during this length of time. When more than one mouse is captured during a trial period, the carcasses are rarely all consumed before the end of the fifteen minutes. Each mouse that was taken or injured by the owl was counted as a capture.

Prey

Four types of deer-mice of different colors were used in the various experiments as prey: "ivory," "discard gray," "buff," and "*blandus* gray." These mice represented different laboratory strains of the single species *Peromyscus maniculatus.* They were, in general, of similar size and of similar type of activity. Their ages varied considerably, but all were of fully adult size. Both males and females were represented, and no attempt was made to discriminate between the two sexes in the records of the number of captures made by the owls.

The "ivory" mice are the result of a recessive mutation which produces a pelage color just slightly more gray than the pure white of the albino strain (Huestis, 1938; Clark, 1938: 2). The ivory mutation was originally discovered by Huestis in a wild mouse of the subspecies *rubidus.* Our animals were taken from the much mixed laboratory population.

The "discard-gray" mice were a rather variable lot of discards from the breeding experiments currently being conducted in the *Peromyscus* laboratory. They were of many different genetic constitutions. Though all were gray in general hue, many different shades of gray were represented. Many of them matched fairly well the color of the gully soil, but others were somewhat darker than this soil.

The "buff" deer-mice used in one experiment (Table V) were the F_1 offspring of a cross between a highly selected strain of *Peromyscus m. blandus* from Tularosa, New Mexico, and various strains of buff mice present in the laboratory. It is probable that the buff character of these laboratory strains was mostly derived originally from the subspecies *nebrascensis,* two stocks of which were involved in their ancestry. *Exiguus, gambeli, rubidus, rufinus,* and perhaps other subspecies also contributed to the ancestry of these buff strains. The *blandus* strain used as one of the parents in the cross was highly inbred and was undoubtedly homozygous for many genes. Presumably, for this reason the buff F_1 offspring were very uniform both in pelage color and in size. Buff being dominant in heredity all the F_1 offspring were buff.

The "*blandus*-gray" mice were the F_1 offspring of a cross between highly inbred, "tipped dark gray" and "tipless gray" strains of *blandus,* both originally from Tularosa, New Mexico. In spite of the inbreeding of the two parental strains of these mice and their consequent considerable amount of homozygosity, the F_1 offspring used in the experiment exhibited moderate variability in shade of pelage. They all had a slight tinge of buffy, and their general hue closely matched that of the Ann Arbor sand, but they were not all alike in shade. On the average they matched to my eyes the shade of the Ann Arbor sand fairly well, but some individuals were paler than the Ann Arbor sand and some were darker.

It will be noted that both the "buff" and the "*blandus*-gray" mice used in the experiment reported in Table V had at least one parent of *blandus* stock from Tularosa. As a result of this similar ancestry these two types of mice were very similar in size and in amount of activity and differed, so far as could be observed, only in their pelage color.

The ivory mice were the palest in pelage of the deer-mice used in these experiments as is shown by their high reflection meter readings (Table II).

TABLE II

COLORS OF FLAT SKINS OF DEER-MICE USED IN THE EXPERIMENTS

Type of Mouse	Specimens	Reflection Meter Readings Means and Extremes		
		Red	Green	Blue
Ivory				
Dorsal stripe	5	64.40 (62–68)	49.40 (46–53)	39.00 (37–41)
Side stripe	5	70.00 (67–74)	56.00 (52–62)	45.00 (41–49)
Buff				
Dorsal stripe	15	18.20 (14–24)	8.93 (6–12)	6.80 (6– 8)
Side stripe	15	29.53 (22–35)	13.07 (10–16)	9.40 (8–11)
Blandus-gray				
Dorsal stripe	9	15.33 (13–18)	10.78 (8–13)	9.22 (6–11)
Side stripe	9	27.89 (21–31)	19.56 (14–23)	17.00 (11–20)

The buff mice averaged higher in readings for reflected red than did the *blandus*-gray mice, both on the dorsal stripe and on the side of the body. In readings for reflected green and reflected blue, on the contrary, the *blandus*-gray mice averaged the higher. This shows that the buff mice had a redder, more buffy hue than did the *blandus*-gray individuals, although the general shade of color was slightly paler in the *blandus*-gray than in the buff mice.

Because of the considerable variability in hue and in shade of the discard-gray mice, no attempt is made to present photometer readings of their pelage color. In every case, however, the discard-gray mice were much darker than the ivory mice against which they were tested.

Mouse "Jungles"

When the floor of the reaction room was bare of obstructions, the owls that served as predators in these experiments were able, as has already been mentioned, to capture living deer-mice in complete darkness. The owls presumably were able to do this through the sense of hearing. Various expedients were tried to prevent the owls from capturing the deer-mice by hearing alone and to force them to use the sense of sight. After many failures to achieve this end, I contrived a mouse "jungle" in which the owls almost never caught a mouse in complete darkness, but only when the light was of an intensity under which it had earlier been demonstrated that the owls could see and find dead mice of this species (Dice, 1945).

The mouse "jungles" were constructed of wooden sticks screwed together to form an open latticework. Sticks three-fourth by three-fourth inches in size and mostly twelve inches in length were placed vertically in a checkerboard pattern, with the sticks spaced eight inches apart on their centers. These vertical posts were connected by horizontal pieces of rough, split lath, three-eighth by three-fourth inches in cross section, which were placed three and one-half inches above the floor in one direction and four and one-half inches above the floor crosswise above the first set of sticks. The space above the floor of the reaction room was thus broken up by the "jungle" into little cells, the largest horizontal dimensions of any opening being a little less than eight by eight inches.

The sticks making up each "jungle" were painted to match the color of the soil of the compartment, so that should a mouse climb up on the sticks he would not be any more or less conspicuous than if he remained on the floor.

In the "jungle" the mice could run freely about under the latticework of horizontal sticks, the only obstructions to their progress being the vertical posts. Although the mice were exposed to attack by the owls, they were nevertheless protected to some extent, because of the handicap imposed on the predator by the presence of the sticks. An owl could reach through the meshes between the latticework formed by the sticks and could catch the mice fairly readily when the light intensity was sufficiently high for him to see his prey.

Although the owl undoubtedly could hear the mice running about under the "jungle," he evidently could only rarely secure them without the aid of sight. Observations were made of the method by which owls secure mice on an unobstructed floor: the wings usually are used to enfold the mice and draw them within reach of the talons. Presumably, this is the manner in which mice are caught in complete darkness after their general position has been located by hearing. In the "jungle," however, this method of capture could not be employed because of the presence of the sticks. The owl, accordingly, was forced to depend on sight for securing the prey. The "jungle," therefore, probably reproduced to a considerable extent the conditions in nature when the prey is moving about among such obstructions as shrubs or herbs.

RESULTS OF THE EXPERIMENTS WITH OWLS AND DEER-MICE

When ivory and discard-gray mice were exposed to the barn owl on silica sand and on gully soil on alternate nights, without any protection, either by a "jungle" or otherwise, 82 conspicuous and 70 concealingly colored mice were taken in 120 fifteen-minute trials (Table III). Approximately as many mice per period, however, were taken in complete darkness and in extremely dim light as were taken under illuminations in which the owl undoubtedly could see his prey. In darkness the owl certainly must have caught mice without using the sense of sight. The selection index against the conspicuous mice in the whole experiment is 0.079, but this is statistically not significant.

With the lack of any protection for the mice in this experiment the owl evidently was able to capture his prey by some sense other than vision. This is demonstrated by the fact that the owl was able to catch the mice in complete darkness. It may be presumed that hearing was the major sense employed to locate the prey, at least in darkness and in very dim light. The failure of the owl in this experiment to show any considerable tendency to select the more conspicuously colored mice is undoubtedly due to his lack of dependence upon sight for the capture of his prey.

TABLE III

Selection of Ivory and Discard-gray Deer-mice by Barn Owl

Floor of selection room bare; no protection for mice. Four live mice of each of two colors exposed in same compartment for each trial; ten trials on each soil type; fifteen-minute periods.

Illumination in Foot Candles (Approximate)	Mice Taken					Conspicuous Mice Taken	Concealingly Colored Mice Taken
	On Silica Sand		On Gully Soil		Average per Trial		
	Ivory	Discard-gray	Ivory	Discard-gray			
0.000,003,5	8	6	5	3	1.10	11	11
0.000,002,0	5	9	7	6	1.35	16	11
0.000,000,53	5	9	7	2	1.15	16	7
0.000,000,31	7	6	10	11	1.70	16	18
0.000,000,08	8	4	7	3	1.10	11	11
Dark	6	5	7	6	1.20	12	12
Total	39	39	43	31	....	82	70

When in another experiment the mice were given partial protection by placing a wooden "porch" over the entrance to the next box, there was still little indication of the selection of mice of any particular pelage color. Presumably, the owl awaited and captured whatever mouse first wandered outside the protective cover of the "porch." The color of the mouse first exposed and consequently caught was a matter of chance.

A series of experiments was then carried out with a two-foot wide "jungle" of sticks, constructed as above described, around the outside of each compartment, leaving the middle of the compartment open. Four each of ivory and of discard-gray mice were exposed to the owl for fifteen-minute periods on silica sand and gully soil on alternate days.

Under these conditions the barn owl demonstrated a striking selection of the more conspicuous mice (Table IV). The selective effect was evident at every light intensity tested, except darkness, the dim light of 0.000,000,31 foot candle, and under the relatively bright light of 0.017 foot candle. The number of mice taken per period was relatively low under the brighter intensities used in the experiments, evidently because the mice in these relatively bright lights remained inside their nest boxes and, therefore, only infrequently exposed themselves to the owl. Nevertheless, selection is indicated to be generally effective over the whole range of light intensities from 0.24 to 0.000,000,08 foot candle.

If the number of mice taken in the whole experiment is added, omitting only those taken in complete darkness, it is found that 124 conspicuously colored mice and 68 that were concealingly colored were taken. The index of selection is 0.292, and the chi-square of the deviation from a 1:1 ratio is 16.333, a highly significant amount. There is no significant difference between the numbers of discard-gray and of ivory mice taken, nor between the numbers taken on silica sand and on gully soil. Neither is there any important difference between the selection indexes on the silica sand and on the gully soil, these being respectively, 0.289 and 0.294.

TABLE IV

SELECTION OF IVORY AND DISCARD-GRAY DEER-MICE BY BARN OWL

"Jungle" of sticks around outside of each compartment. Four live mice of each of two colors exposed in same compartment for each trial; ten trials on each soil type; fifteen-minute periods.

Illumination in Foot Candles (Approximate)	Mice Taken					Conspicuous Mice Taken	Concealingly Colored Mice Taken
	On Silica Sand		On Gully Soil		Average per Trial		
	Ivory	Discard-gray	Ivory	Discard-gray			
0.24	1	4	3	1	0.45	7	2
0.017	4	2	3	1	0.50	5	5
0.004,8	1	4	4	1	0.50	8	2
0.001,4	2	11	9	7	1.45	20	9
0.000,10	7	7	11	3	1.40	18	10
0.000,026	4	6	6	4	1.00	12	8
0.000,013	3	7	7	6	1.15	14	9
0.000,003,5	......	4	7	1	0.60	11	1
0.000,002,0	2	5	4	5	0.80	9	7
0.000,000,53	1	1	2	1	0.25	3	2
0.000,000,31	4	4	2	2	0.60	6	6
0.000,000,08	3	3	8	4	0.90	11	7
Dark	1	.....	1	2	0.20	1	3
Totals	33	58	67	38	....	125	71
Totals omitting "dark" ...	32	58	66	36	....	124	68

The fact that four mice were taken in darkness in twenty trials shows that in this experiment the owl was able to capture a mouse occasionally by some sense other than sight. Presumably, most or all of these mice were captured in the middle of the room, where they were not protected by the "jungle." Tracks in the sand indicated that at least one mouse actually was captured in this open space.

The barn owl in this experiment was able to capture mice readily under an illumination as dim as 0.000,000,08 foot candle. He was actually very successful in this light intensity in capturing live mice (0.90 per fifteen-minute period), though in an earlier experiment he had failed to find dead mice in such very dim light (Dice, 1945 : 398). Moving objects are probably seen by the owl more readily in very dim light than are stationary ones. Furthermore, the owl can probably determine the general location of a live mouse by the sounds it produces in moving about. These considerations may explain why this owl was able to secure live mice in such very weak light, whereas he had previously failed to find dead ones.

The experiment with the mice partly protected by a "jungle" of sticks extending around the outside border of each testing compartment was then repeated, with the long-eared owl as the predator (Table V). This bird was more timid than was the barn owl and did not secure as many mice per trial period of fifteen minutes. However, he took more of the conspicuous than of the concealingly colored mice over a wide range of light intensities extending from 0.002,3 to 0.000,003,5 foot candle. At intensities of 0.000,6, of 0.000,1, of 0.000,002, and of 0.000,000,53 foot candle, however, the owl took more of the concealingly colored than of the conspicuous mice, though in each case the number of individuals taken was small. In complete darkness the owl secured one mouse in twenty trials, but it seems likely that this mouse was taken at the instant just after the lights were turned on, for the owl was then discovered on the floor of the room with a newly captured mouse in his talons.

If all the mice taken in this experiment at all the light intensities are added together, omitting only the mouse taken in darkness, then forty-three conspicuously colored mice and twenty-six concealingly colored mice were taken. The selection index against the conspicuously colored mice is 0.246. The chi-square of the deviation from a 1 : 1 ratio is 4.188, which is barely significant, presumably because of the few mice included in the counts. The difference in the numbers of mice taken on the silica sand and on the gully soil, respectively, is not significant. Of the ivory mice, however, forty-six were taken against only twenty-four of the discard-grays. The chi-square of the difference is 6.914, which is highly significant, showing that the owl had a preference for the ivory mice.

In order to measure the effectiveness of selection when there is only a small amount of difference between the colors of two contrasting kinds of prey, another experiment was then performed using buff and *blandus*-gray mice. The barn owl was used as the predator, and the mice were exposed as before for fifteen-minute periods. In this experiment, however, the "jungle" of interlaced sticks was extended to cover the whole floor of each testing compartment, excepting only the area occupied by the metal nest boxes of the mice. The gully soil placed in the one compartment closely matched the color of the buff mice, but the Ann Arbor sand in the other

TABLE V

SELECTION OF IVORY AND DISCARD-GRAY DEER-MICE BY LONG-EARED OWL

Partial ''jungle'' around outside of each compartment. Four live mice of each of two colors exposed in same compartment for each trial; fifteen-minute periods.

Illumination in Foot Candles (Approximate)	Mice Taken									Conspicuous Mice Taken	Concealingly Colored Mice Taken
	On Silica Sand				On Gully Soil				Average per Trial		
	Ivory		Discard-gray		Ivory		Discard-gray				
	Trials	Taken	Trials	Taken	Trials	Taken	Trials	Taken			
0.002,3	5	......	5	1	7	1	7	1	0.25	2	1
0.001,4	4	1	4	2	5	......	5	......	0.33	2	1
0.000,60	9	2	9	2	8	......	8	1	0.29	2	3
0.000,10	6	3	6	......	6	2	6	......	0.42	2	3
0.000,026	10	4	10	......	10	8	10	......	0.60	8	4
0.000,013	10	2	10	3	10	10	10	......	0.75	13	2
0.000,003,5	10	3	10	5	10	7	10	3	0.90	12	6
0.000,002,0	6	1	6	1	5	......	5	2	0.36	1	3
0.000,000,53	6	1	6	......	6	1	6	2	0.33	1	3
Dark	10	......	10	......	10	......	10	1	0.05	0	1
Totals	76	17	76	14	77	29	77	10	....	43	27
Totals omitting ''dark''	66	17	66	14	67	29	67	9	....	43	26

compartment did not so closely match the color of the *blandus*-gray mice. Only one light intensity was used, calculated to be 0.000,10 foot candle. In 176 trials, 107 conspicuous and 65 concealingly colored mice were taken (Table VI). The index of selection against the conspicuous mice is 0.244. The chi-square of the deviation is 10.256, which indicates high significance. There is no significant difference between the number of mice of either color taken in the experiment, nor between the numbers which were taken on the two colors of soil.

An important difference in rate of selection, however, appears in this experiment to be correlated with the color of the soil. On the gully soil fifty-five of the conspicuous *blandus*-gray mice were taken, and only twenty-five of the concealingly colored buff mice. The index of selection here is 0.375, and the chi-square is 11.250, which is highly significant. On the Ann Arbor sand fifty-two of the conspicuous buff mice were taken and forty of the presumably concealingly colored *blandus*-grays. The selection index on this soil was only 0.130, and the chi-square only 1.565, which is not significant. The cause of the difference in rate of selection on these two colors of soil is believed to be the better match in color of the buff mice to the gully soil than that of the *blandus*-gray mice to the Ann Arbor sand. It has been pointed out that the *blandus*-gray mice were variable in shade of color, so that some of them did not well match the color of the Ann Arbor sand.

TABLE VI

SELECTION OF BUFF AND *BLANDUS*-GRAY DEER-MICE BY BARN OWL

A complete "jungle" over the whole floor of each compartment. Four live mice of each of two colors exposed in same compartment for each trial; forty-four trials on each soil type. Illumination calculated to be 0.000,10 foot candle.

Mice Taken				Conspicuous Mice Taken	Concealingly Colored Mice Taken
On Gully Soil		On Ann Arbor Sand			
Buff	*Blandus*-gray	Buff	*Blandus*-gray		
25	55	52	40	107	65

These experiments with owls and deer-mice demonstrate that when live deer-mice are exposed on the bare floor of a room without protection of any kind, owls of two species are able to capture them in complete darkness, presumably by the sense of hearing. In every experiment, however, in which the owl was in considerable part dependent upon the sense of sight for capturing his prey, the greater proportion of animals captured was of a color contrasting with that of the background.

In those experiments where the mice were given the protection of a "jungle" of sticks, simulating the protection given to the mice in nature by the vegetation, the selection index in favor of the concealingly colored mice over those that contrasted in color with their background ranged from

0.24 to 0.29. The deviation of the selection index from zero is highly significant in the two experiments in which the barn owl served as the predator. In the one experiment in which a long-eared owl served as the predator the deviation of the selection index from zero is only barely significant (chi-square = 4.188), probably because of the small number of mice involved.

EXPERIMENTS BY SUMNER ON THE SELECTION OF FISH

The best measurements previously published of the effectiveness of selection under carefully controlled laboratory conditions are those of Sumner (1934, 1935*a,* 1935*b*). Sumner did not estimate the effective rate of selection shown by his experiments, but this may be calculated from his figures. In his experiments on the selection of dark-background-adapted and pale-background-adapted mosquito-fish (*Gambusia patruelis*) by the Galapagos penguin, 366 fish were eaten that contrasted in color with their background and 176 that were more or less similar to the shade of their background (Sumner, 1934). If four fish that were of doubtful color are ignored, the total number of fish taken was 542. The selection index against the conspicuous fish is 0.351, and the chi-square of the deviation is 6.661, which is highly significant.

Similarly, when a night heron was used as the predator, 223 conspicuous and 140 protectively colored fish were eaten or injured (Sumner, 1935*a,* Table 2). The selection index in favor of the protectively colored animals is 0.229, and the chi-square is 18.978.

In those experiments in which a sunfish (*Apomotis cyanellus*) was used as the predator only those tests in which the numbers of the two color types of mosquito-fish were equal and in which they were exposed to the predator without a waiting period will be considered (Sumner, 1935*b*: Table 1, experiments 1–4, 9–12, 14, 18, 19, 23, 28). Under these conditions, 166 conspicuously colored and 79 concealingly colored prey were taken. The selection index against the conspicuous fish was 0.355, and the chi-square of the deviation is 30.894.

In these experiments of Sumner the selection index against the animals that were conspicuous when viewed against their backgrounds ranged from 0.23 to 0.36. This is a very considerable amount of selection against the conspicuous fish as compared to the concealingly colored ones. In every experiment the deviation of the selection index from zero is statistically highly significant.

EXPERIMENTS BY ISELY ON THE SELECTION OF ACRIDIANS

Isely (1938) studied the selection of various grasshoppers and other acridians by domestic and wild birds. The prey were sometimes picketed out alive and sometimes were anesthetized. They were exposed in the various experiments to the attacks of bantam chickens, a domestic turkey, English sparrows, mockingbirds, and other birds. Soils of several colors were prepared on plots about sixteen by sixteen inches square arranged in a checkerboard pattern in an open yard at Waxahachie, Texas. The soil colors employed were white, black, red, and green, the last being produced by a cover of vegetation. The acridians used were ordinarily exposed in matched pairs of species, each member of the pair being recorded as being "protected" or "nonprotected" in coloration on the soil concerned.

Inasmuch as different species of acridians were compared when exposed on the various colors of soil, these experiments by Isely were not as carefully controlled as were those of Sumner and of myself, where the two types of prey offered were always of the same species. Where different prey species are compared it is always possible that some difference in their size, shape, or behavior might influence the selection. Furthermore, the soils used by Isely were of several types, on only one of which the particular prey species concerned was concealingly colored. Nevertheless, these experiments are of great interest and value in that a diversity of predators and of prey species were utilized.

Each of the types of predators employed took a greater number of the nonprotected than of the protectively colored species of acridians (Isely, 1938: Table 5). The total of nonprotected acridian individuals taken in all the experiments was 405 and of protectively colored individuals was 183. The selection index against the nonprotected individuals is 0.378, and the chi-square of the index is 83.816.

DISCUSSION

The experiments above described in which owls served as predators and deer-mice as prey demonstrate that on bare ground the barn owl and the long-eared owl are able to capture living prey without the use of vision, presumably by the sense of hearing. Other experiments not previously reported have demonstrated that the barred owl (*Strix varia*) also is able to capture live deer-mice in complete darkness on the bare floor of the reaction room.

In nature, however, wild mice usually avoid open spaces and keep under vegetation, rocks, and other "cover." Although the sense of hearing must be of great value to owls in locating the general position of their prey, it is very doubtful if in nature the sense of hearing alone would suffice for making the actual captures. The well-developed eyes that owls possess and their demonstrated ability to see in very weak light indicate that sight is an important factor in their ecology. It seems certain, therefore, that to secure their prey under natural conditions owls must usually depend heavily on sight.

Birds and teleost fishes both have color vision (Walls, 1942), but it cannot be demonstrated that the predators employed in the experiments by Sumner and myself actually made use of contrasts in hue in capturing their prey. Many of the experiments with the owls were performed under illuminations so weak that the birds could not be expected to discriminate colors. Even in those experiments where there was a difference in hue as well as in shade between the two types of prey offered the owl, it seems probable that the choice must have been based on the difference in shade rather than on the difference in hue. It is noteworthy, nevertheless, that the owls tended to select those mice that to human eyes were conspicuous in hue as well as in shade when viewed against their background of soil.

The range of nocturnal light intensities over which the owls select deer-mice that are conspicuous in color is very extensive. In one experiment with the barn owl (Table IV) selection was indicated to be operative over the whole range of light intensities from just below an illumination at which the mice would be inactive due to the light being too bright, down to the lowest light intensity at which the owl probably could see his prey. The evidence from the long-eared owl is less conclusive (Table V), but indicates that selection for the more conspicuous mice occurred over a considerable range of illuminations.

Within some certain range of light intensities it is possible that the selection of deer-mice by owls may be more intense than under either weaker or stronger illuminations. The previous study of the ability of owls to find dead prey in weak illuminations showed that over a long range of decreasing illuminations these animals have increasing difficulty in finding their food (Dice, 1945). It might be assumed, therefore, that selection should be most discriminating at those light intensities where the predator is just barely able to see his prey. The data available, however, are not sufficient to prove such an effect.

Whether or not selection may be more intense at some intensities of illumination than at others, it is indicated by these experiments that natural selection should be operative under almost any illumination to which deer-mice would likely be exposed in nature.

The difference in pelage color between the ivory and the discard-gray mice used in certain of the experiments (Tables III–V) seems to our eyes to be much greater than that between the buff and the *blandus*-gray mice used in the last described experiment (Table VI). Nevertheless, the selection indexes did not differ very greatly in these several experiments. This may in part be due to the fact that in the experiments with the ivory and discard-gray mice the middle of the testing compartment was bare and was not covered by the mouse "jungle." Some mice were certainly taken in the open area in the middle of the compartment and if these animals were taken without the use of sight, this may have tended to decrease the apparent effectiveness of selection against the conspicuous ivory mice. Furthermore, the amount of data obtained, even with these laborious experiments, is inadequate for statistical comparison.

The difference in pelage color between the buff and the *blandus*-gray mice used in the one experiment (Table VI) is no greater than the differences that in nature distinguish certain subspecies and local races of *Peromyscus*. In areas of intergradation between subspecies and in many other situations, the populations of these deer-mice may be composed of various proportions of two or more color varieties. In fact, buff and gray color phases are conspicuous in the wild populations of the deer-mice of the subspecies *blandus*. It has already been demonstrated that the buff and gray color phases of *blandus* are due to a single gene difference, buff being dominant to gray (Dice, 1933). Furthermore, in the native region of *blandus* in southern New Mexico various colors of soils occur, some of which roughly resemble the gully soil and Ann Arbor sand, respectively, used in this experiment. In many habitats in nature, therefore, the conditions for the incidence of selection closely parallel those provided in the laboratory experiments here reported.

In every population of *Peromyscus* much of the variability that exists has a basis in heredity (Sumner, 1932; Dice, 1940). The variability within populations in pelage color and in other inherited characters provides natural selection with an abundance of materials on which to operate. It is impossible to escape the conclusion that natural selection by predators must be an important factor in the evolution of pelage color in these deer-mice in any region where they are subject to predation by owls or by other predators with similar visual acuity.

The selection indexes in those experiments in which the barn owl and long-eared owl were forced to depend largely on sight for the capture of their deer-mouse prey ranged from 0.24 to 0.29. In the experiments by Sumner, in which mosquito fish were used as prey and the Galapagos penguin, the night heron, and the sunfish were predators, the selection indexes were, respectively, 0.35, 0.23, and 0.36. Isely's experiments on the selection of acridians by birds gave a selection index of 0.38. The similarity in the magnitudes of these indexes, irrespective of the kind of predator or the type of prey, is surprising. The deviations of the indexes from the zero value expected of a 1 : 1 ratio in the absence of selection is in every case statistically significant and in most of the experiments the chi-square values of the deviations are high.

The most striking feature of all the laboratory experiments here described is the very great advantage the concealingly colored individuals of the prey species have over the conspicuous individuals in escaping capture by predators. In every experiment in which the predator was evidently using sight to capture his prey, the concealingly colored individuals enjoyed more than a 20 per cent advantage over the conspicuous animals in escaping capture. In one of the experiments reported by Sumner the advantage of the concealingly colored individuals amounted to as much as 36 per cent, and in the experiments by Isely the advantage was 38 per cent.

Such a high rate of selection, should it be applied to a natural population, would undoubtedly result in a very rapid change in the frequencies of the genes producing the character under selection. If natural selection operates in nature with anything like the effectiveness indicated by these experiments and if the trend of selection is generally in the same direction, evolution should proceed very rapidly whenever and wherever a variable form is exposed to its action.

SUMMARY

Experiments are described in which it is attempted to measure the rate of selection under controlled laboratory conditions when the barn owl (*Tyto alba pratincola*) and the long-eared owl (*Asio wilsonianus*) serve as predators and the deer-mouse (*Peromyscus maniculatus*) as prey. Equal numbers of two different color varieties of the mice were exposed to the owls for a series of fifteen-minute periods. In most of the experiments a ''jungle'' of interlaced thin sticks gave partial cover to the mice. The mice were exposed alternately on two colors of soil, one type of which matched the color of one variety of mouse and the other soil that of the other kind of mouse.

On the floor of a room free of obstructions the owls are able to capture live deer-mice in complete darkness, presumably by the sense of hearing. Under the partial protection of a ''jungle'' of sticks, however, the owls seldom were able to catch mice except under illuminations at which it had earlier been demonstrated that they can see.

A selection index is proposed to measure the effectiveness of selection. In a situation where two types of prey, A and B, are available in equal numbers, if the numbers taken are respectively, a and b, then the selection index of A is $a-b/a+b$. The selection index may vary between $+1.0$ and -1.0, being zero in the absence of selection. The significance of any given selection index may be tested by chi-square.

In those experiments in which the owls were forced to depend very largely on sight for capturing the deer-mice the selection indexes in favor of the concealingly colored mice ranged from 0.24 to 0.29. Selection occurred over a wide range of illuminations, extending from about the lower limit at which owls are able to see their prey to an intensity of light above which these nocturnal mice usually become inactive. In an experiment in which buff and gray mice with pelage colors similar to those that distinguish races in nature were used as prey, a selection index of 0.24 was obtained in favor of the mice that were inconspicuous when viewed against their backgrounds.

The experiments performed some years ago by F. B. Sumner on the selection by several kinds of predators of light-adapted and dark-adapted mosquito fish give selection indexes ranging from 0.23 to 0.36. The experiments by Isely on the selection of acridians by various kinds of birds show a combined selection index of 0.38.

From the very high possible rates of selection indicated by these experiments, it is concluded that natural selection can theoretically produce very rapid evolution whenever a genetically variable population is exposed to its action.

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